



LINKAGE STUDIES IN BARLEY

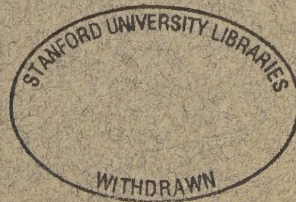
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LINKAGE STUDIES IN BARLEY¹

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INTRODUCTION

The present conception of the chromosome theory of heredity is that the genes are arranged in a stable, orderly, linear manner in the chromosome; that genes in separate chromosome pairs are inherited independently and that there is the same number of groups of linked genetic factors as homologous pairs of chromosomes. The degree of linkage is in general considered to be correlated directly with the distance apart of the factors in the chromosome. *Drosophila melanogaster* has four pairs of chromosomes and some 400 factors have been located in them. Maize which has been studied more extensively than any other cereal crop has more than 35 factors located in eight of the ten pairs of chromosomes. With other cereal crops only a few isolated groups have been observed. There are a considerable number of easily distinguishable character pairs in cultivated barley and only 7 pairs of chromosomes. Barley can be grown satisfactorily under many different environmental conditions and for these reasons it appears desirable to use this organism in studies of linkage relations.

Arrangements have been made whereby the Minnesota, Colorado and Oklahoma stations are cooperating in studying linkage relations in barley. The present paper is a report of studies conducted in Colorado.

REVIEW OF LITERATURE

A fairly extensive review of the published papers on linkage relations in barley was made by GRIFFEE (1925) and only those papers which have a direct bearing on the present studies are reviewed.

Chlorophyll Deficiencies

An albino seedling is reported by WIEBE (1924) which was found in the F₃ head row of a cross between Nepal and a many noded dwarf. From later studies it was concluded that this Albino was due to a single

recessive factor. NILSSON-EHLE (1922) describes six chlorophyll mutations. Albino Nos. 1 and 3 occurred in six rowed barleys and Albino No. 2 in a two rowed variety. Yellow No. 1 was found in a six rowed barley and Yellow No. 2 in a two rowed form. Chlorina, a pale green chlorophyll deficient type, occurred in Gold, a two rowed barley. All of the whites are recessive to green and the progeny of the selfed heterozygous green plants segregated in a simple Mendelian ratio of 3 green seedlings to 1 white. A linkage was found between Albino 3 and Chlorina. All of the other chlorophyll deficiencies were found to be independently inherited.

HALLQVIST (1926) made crosses between the following chlorophyll deficiencies: Albino 1, Albino 2, Albino 4, Xantha 1, Xantha 2, Chlorina, Superchlorina, Virescent 1, Virescent 3, Lutescens 1, and the abnormalities Dwarf and Linearis. Forty-two out of 78 possible combinations were made. In crosses involving different albinos a ratio of green to albino of 9 to 7 was obtained and in a cross between a virescent and a xantha; green, xantha, and virescent seedlings occurred in a ratio of 9:3:4. In crosses in which Dwarf 1 was used a deficiency in the number of Dwarfs was found. This was explained by the fact that the Dwarf gametes in fertilization take part in fewer numbers than the normal gametes. In one combination the obtained ratio comes very close to the calculated with a deficit of 28 percent in the Dwarf gametes. The linkage of Albino 3 and Chlorina, found by NILSSON-EHLE, was confirmed and a linkage of Albino 4 with Albino 3 and Chlorina was found. The crossover percentages were found to be 10.2 for Albino 3 and Chlorina, 3.8 between Chlorina and Albino 4 and 12.5 between Albino 3 and Albino 4. The same author (1923) observed the effect of different temperatures on the development of chlorophyll in a yellowish white seedling. At a temperature of about 5°C no chlorophyll was developed. At a temperature between 12°-15°C, the seedlings produced chlorophyll in the tips of the leaf. After several days the chlorophyll deficient seedlings died. In temperatures of about 20°C, the lack of chlorophyll could not be detected in the young seedlings. The plants that developed past the seedling stage presented a somewhat stunted appearance. In some cases ears were formed but in many cases these were abnormal.

COLLINS (1927) describes an albino which can be differentiated at temperatures lower than 45°F. When grown at temperatures above 65°F, no albino plants develop. A single recessive gene is responsible for this chlorophyll deficient type. The F_2 segregation from the cross

six rowed albino $\times$ two rowed non-albino shows independent inheritance for the factor pairs concerned.

Inheritance of other characters

HAYES and GARBER (1927) summarize the literature on inheritance of the lateral florets as follows: "Two general results have been obtained from crossing two and six-rowed varieties. The most frequent result is an intermediate condition in the F_1 in which the lateral florets are awned, but produce little or no fruitfulness. In F_2 a 1:2:1 ratio of six-rowed, intermediate, and two-rowed forms are obtained. Six- and two-rowed forms breed true to these respective characters in later generations. Results of this nature can easily be explained on a single main factor difference. A cooperative study carried on at the MINNESOTA EXPERIMENT STATION has shown the probable origin of some *intermedium* forms. In a cross between Manchuria, a six-rowed barley, and Svanhals, a two-rowed variety, the F_1 was slightly fruitful and produced intermediate awns on the lateral florets. In F_2 a wide range of forms was obtained. The genetic nature of the F_2 plants was determined by growing seed of each in F_3 . From the F_3 results it was possible to classify F_2 plants as follows:

1. Those that bred true for the six-rowed character.
2. Those that segregated, giving six-rowed, awned intermediate forms with very high fruitfulness of the lateral florets and *intermedium* forms in a 1:2:1 ratio.
3. *Intermedium* forms that bred true, giving few or no awns on the lateral florets and producing approximately 50 percent of barren lateral florets.
4. Those that gave all forms as in F_2 .
5. Those that produced intermediates and two-rowed types.
6. Those that produced six-rowed, awned intermediates with little or no fruitfulness in the lateral florets and two-rowed forms in a 1:2:1 ratio.
7. Those that bred true for the two-rowed condition.

Results were explained by considering the Manchuria parent to contain two factors, one for six-rowed and one for *intermedium*, which was hypostatic to the six-rowed factor. It was thought possible that minor modifying factors were sometimes present which influenced the degree of fruitfulness of the lateral florets. Crosses between *intermedium* and six-rowed forms gave intermediates of high fruitfulness in F_1 and a ratio in F_2 which indicate a single factor difference. *Intermedium* forms crossed

with two-rowed, gave awnless forms with very low fruitfulness in F_1 and a ratio indicating one main factor difference in F_2 .

In a cross of *Hordeum deficiens steudelii* $\times$ Manchuria, GRIFFEE (1925) reports a single factor difference for six-rowed and *deficiens*. In another cross between Svanhals and Lion two main factor pairs were found to be responsible for fertility of the lateral florets. The conclusion was reached that the *intermedium* factor may be carried by a six-rowed variety and that the presence of this factor does not modify the expression of the factor for the six-rowed condition. Two-rowed lacks the factors for intermedium and six-rowed. Apparently the factor pairs which differentiate six-rowed *versus* two-rowed and *intermedium versus* two-rowed are independently inherited.

In a contribution to the genetics and the morphology of barley, VEIDEMAN (1927) states: "The cause of sterility or fertility of the lateral spikelets of barley lies not in the presence or absence of reproductive organs in the lateral florets, as commonly thought but in the structure of the pedicel of the lateral florets, typical for each variety. The longer and narrower the pedicel, the feebler is the development of the lateral spikelet, and the reverse. Thus the fertility is not an independent hereditary character but the physiological results of the anatomical structure and the function of the pedicel. To put it differently: there exists no "gene for fertility."

HOR (1924) concludes that *deficiens*, *distichon* and *vulgare* are multiple allelomorphs. TEDIN and TEDIN (1926) in discussing the type of spike in a cross between a six rowed and a two rowed barley, suggest that the lateral florets with rounded tips be classified as two rowed. Such two rowed plants may produce somewhat inflated lateral florets, but these never bear kernels. Such types breed true for the two rowed condition. When the palea was more or less pointed the plant was classified as heterozygous and has always proved to be heterozygous by the breeding test. In F_3 there are three distinct groups of families, namely, constant six-rowed or two-rowed and families segregating for all three types; no families segregating in typical two-rowed and *intermedium* were observed. Their *intermedium* is similar to the intermediate of HAYES and GARBER (1927).

HAYES and GARBER (1927) list the following characters as being dependent upon single factor differences: Hooded *versus* awned, rough *versus* smooth awn, black palea *versus* colorless, purple palea *versus* colorless, hulled *versus* naked, and black pericarp *versus* white pericarp.

GRIFFEE (1925) found that the characters early heading *versus* late heading and intermediate smooth *versus* smooth awn depend upon single factor differences. HOR (1924) decided that long haired rachilla and short haired rachilla differ by a single genetic factor.

Linkage relations

Several linkage studies have been reported recently in barley and various conflicting results obtained. HAYES and GARBER (1927) give a rather extensive summary of the published data. GRIFFEE (1925) found that resistance and susceptibility to *Helminthosporium sativum* are definitely inherited. By correlating the reaction of F_3 lines to this pathogen in relation to other characters in F_2 the inference is drawn that at least three factors or groups of factors are concerned in the production of resistance of the type possessed by Svanhals. One factor or group of factors for reaction to *Helminthosporium sativum* was linked with the factor for two rowed, one with the factor for rough awn, and one with the factor for white glumes.

The factor for early heading was found to be linked with the factor for six-rowed. The linkage intensity was very low, the crossover value being 42 percent. The linkage for susceptibility to *Helminthosporium sativum* with the factor for earliness is much more intense than that with the factor for six-rowed or else earliness in itself predisposes the plant to attacks by the pathogen. From the results of the studies, four linkage groups have been established. HOR (1924) found that the long and short haired rachilla factors are independent of the allelomorphic series for fertility of the lateral florets and hairiness of the rachilla and hulled *versus* hullless were inherited independently of each other. A linkage is shown between factors for hairy glume and naked and hulled seeds. The percentage of crossing over is calculated as 25.32 ± 1.73 . He also concludes that the factors for black *versus* white glume, rough *versus* smooth awn, and long *versus* short haired rachilla are in one group. Too small a number of individuals were studied in each case to be certain of his conclusions. NEATBY (1926) concludes from studies made on quantitative characters that maturity, height and density are not very closely linked with the factor pair which differentiates two- *versus* six-rowed. TEDIN and TEDIN (1926) found a correlation between the height of plant and the two-rowed type. The two-rowed segregates from a cross between six-rowed and two-rowed were, on the average, 10 cm taller than the six-rowed type. They conclude that this correlation most likely is due to linkage between the factor for two rowedness and a plant height factor.

In a more recent paper (1927) the same authors, in a study of development of the kernel basis and its relation to density, referred to three types of bases: vernum, with a transversal nick; falsum, without a nick, but with the dorsal side bevelled; spurium, without both the nick and the bevelling. The lax-eared nutens as well as the corresponding variety with fertile lateral florets, vulgare, always belong to the falsum type. The dense-eared erectum, as well as the extremely dense-eared zeocriton and the correspondingly dense-eared six-rowed variety hexastichum were all either vernum or spurium. They found that two complementary factors E_{r_1} and E_{r_2} are necessary for the development of the falsum-basis whereas the vernum basis may develop from $E_{r_1}E_{r_1}e_{r_2}e_{r_2}, e_{r_1}e_{r_1}E_{r_2}E_{r_2}$ or $e_{r_1}e_{r_1}e_{r_2}e_{r_2}$. They say in conclusion "In spite of the fact that conclusive proof cannot be given, we consider it highly probable, that E_{r_1} and E_{r_2} are linked with one another, with a crossing over between 33 and 40 percent."

MATERIAL AND METHODS

This paper presents a study of the inheritance of simple Mendelian factor pairs and their possible linkage relations with particular attention to the linkage of certain chlorophyll deficiencies. The following varieties have been used in crosses: Colsess, Trebi, *H. distichon nigrinudum*, Minnesota Selection 90-5, Minnesota Selection 90-8, and *H. deficiens nudideficiens*.

Description of parents

Colsess

This is a six-rowed, hooded barley with a hulled grain of a bluish green color. The straw and glume color is light yellow. The shank of the hood is about 5 mm long and is barbed at the base. The rachis is rather tough and the head does not shatter easily. The rachilla hairs are short and the outer glume is covered with very short hairs.

Trebi

Trebi is described by HARLAN, MARTINI, and POPE (1925) as a pure line selection made in 1907 in the cooperative breeding experiments conducted by the U. S. DEPARTMENT OF AGRICULTURE and the MINNESOTA AGRICULTURAL EXPERIMENT STATION at St. Paul, Minn. It is a six-rowed, bearded, hulled barley with heads very similar to those of Coast. Under Colorado conditions (irrigated) the kernels are large and bluish in color. The straw is weak. In threshing the awns break off from the glume more easily than those of the Coast variety.

Hordeum distichon nigrinudum (HARLAN 1918)

This is an awned, two-rowed barley, with a hullless black grain and black glumes. The naked seeds have a charred appearance. The straw color is purple which is most marked in the sheath of the leaves of the upper node. The rachilla hairs are short.

Minnesota Selection 90-5

This is a two-rowed barley of the distichon type. It has black, smooth awns. The grain and glumes are black, the rachilla hairs are long and the central rib of the outer glume has long fine hairs.

Minnesota Selection 90-8

This is similar to Minnesota Selection 90-5 with the exception that the head is a little more lax.

H. deficiens nudideficiens (HARLAN 1918)

This variety is a rough awned, two-rowed barley with a hullless grain. The grain is colorless, the rachilla hairs are long and the rachis is tough. Under Colorado (irrigated) conditions this barley is very early.

Methods of conducting experiments

In this study of the various differential characters particular attention has been given to certain chlorophyll deficiencies. As plants which are homozygous recessive for the chlorophyll defective seedling factors cannot be grown to maturity, plants heterozygous for genetic factors for green and white seedlings were used as one or both of the parents. When one parent was heterozygous for green and white seedlings, two types of F_1 plants were obtained; one being homozygous for the green seedling factors and the other heterozygous for the green and white seedling factors. In crosses in which both parents were heterozygous for different chlorophyll deficiencies four types of F_1 plants were obtained.

By testing seedling progeny of F_1 plants in the greenhouse, it was possible to determine fairly accurately their genetic nature for chlorophyll deficiencies. Particular genetic types were used to make more extensive studies in the later generations.

Studies of inheritance of botanical character differences were made for the most part in crosses where chlorophyll deficiencies were not involved.

INHERITANCE OF SIMPLE MENDELIAN CHARACTERS

White seedlings in Colsess

Head selections were made in the F_{11} generation of Colsess barley in 1922. The progeny of several of the selections were noticed to contain white seedlings. These seedlings died in about a week or ten days after germination. Counts of white seedlings were made in the F_{12} generation in three strains which were later numbered, Colsess I, Colsess II, and Colsess III. The observed ratios of green to white seedlings in the F_{12} generation were very close to a 3 to 1 ratio. The deviation divided by the probable error¹ was 1.7 in the case of Colsess I; 0.98 in the case of Colsess II, and 2.6 in the case of Colsess III. Progeny from seed of these plants were tested for white seedlings in the greenhouse in F_{13} . From these studies the following conclusions were drawn. Colsess No. III agrees very well with a 3 to 1 ratio of green to white seedlings on the basis of data from the F_{12} and F_{13} generation. The segregation obtained from Colsess I fits closely to a 3 to 1 ratio of green to white seedlings in the F_{12} and F_{13} generation. Colsess No. II, while indicating a 3 to 1 ratio of green to white seedlings, later developed a strain which approaches more closely to a 9 to 7 ratio. This latter strain was not used in the linkage studies.

In the F_1 generation of crosses between Colsess I and Colsess III, white seedlings appeared. This indicates that these two lines are dependent upon the same genetic factors for white seedlings. In crosses between Colsess I and Colsess II and between Colsess II and Colsess III similar results were obtained. The number of homozygous and heterozygous F_2 lines from crosses where both parents were heterozygous for white seedlings is given in table 1. In all cases where the parent plants used in the crosses were heterozygous for white seedling factors both green and white seedlings were obtained in the F_1 . This again indicates that the white seedlings in Colsess I, II, and III are the result of the reaction of the same factor pair. This is further borne out by studying the progeny of heterozygous F_1 plants.

With the exception of crosses No. 58 and 59 the fits are good to the expected 3 to 1 ratio. The number of white seedlings in cross No. 59 is low. In cross 58D, divided by P.E. was 10.86 and the number of white seedlings was much larger than expected on a 3 to 1 basis. In conclusion it can be stated that the white seedlings in all crosses involving Colsess I,

¹ Tables of probable errors of Mendelian ratios prepared by the Department of Plant Breeding of CORNELL UNIVERSITY, Ithaca, New York, were used to determine the probable errors.

II, and III, except cross No. 58, are due to the reaction of the same factor pair.

TABLE 1

Seedling counts in the F₁ generation of Colseß×Colseß crosses and the number of segregating and pure green families in the F₁.

CROSS	CROSS NUMBER	F ₁ SEGREGATION		NUMBER OF F ₁ SEGREGATING FAMILIES	NUMBER OF F ₁ PURE GREEN FAMILIES
		Green	White		
Colseß I × Col. II	12	8	8	5	3
Colseß I × Col. II	59	13	2	7	4
Colseß I × Col. III	92	11	3	5	6
Colseß I × Col. III	91	10	6	7	3
Colseß I × Col. III	15	11	4	7	4
Colseß III × Col. II	350	10	6	6	4
Colseß III × Col. II	352	10	5	7	4
Colseß II × Col. III	50	12	4	6	6
Colseß II × Col. III	58	10	5	8	3
Observed Total		95	43	58	37
Calculated Total		103.5	34.5	63.34	31.67

A cooperative agreement has been reached by several workers to accept *aa* which was first used by NILSSON-EHLE to denote the genotypes of white seedlings in barley. NILSSON-EHLE subscribes his letters with the numbers 1, 2, etc., to denote genetically different whites. Until such times

TABLE 2

Segregation in F₂ for green and white seedlings in crosses between the different Colseß strains.

CROSSES	CROSS NUMBER	OBSERVED RATIO		DEVIATION IN NUMBERS	D — PE
		Green	White		
Colseß I × Col. II	12	80	26	0.5	0.17
Colseß I × Col. II	59	1936	584	46.0	3.14
Colseß I × Col. III	92	143	39	6.5	1.65
Colseß I × Col. III	91	223	67	5.5	1.11
Colseß I × Col. III	15	1257	384	26.25	2.22
Colseß III × Col. II	350	94	37	4.25	1.27
Colseß III × Col. II	352	171	57	0	0
Colseß II × Col. III	50	801	272	3.8	0.40
Colseß II × Col. III	58	2012	898	170.5	10.85

as the white seedlings are tested with NILSSON-EHLE's material, a letter representing the variety in which the particular whites first occurred will be used as a subscript to denote a particular white seedling. If more than one white occurs in a variety, a subscript to the letter will be used until

it is identified with a white in some other variety. Thus the factor pair for the white seedling condition in the Colsess strains is designated as $A_c a_c$.

Cross No. 58 which deviated widely from a 3:1 ratio of green to white was studied in later generations. The different segregations of the F_2 plants from this cross are presented in table 3.

TABLE 3

The observed segregation in F_2 compared with calculated 3:1 and 9:7 ratios of white and green seedlings in Cross No. 58.

FAMILY NUMBER	NUMBER SEEDLINGS	3:1 RATIO		DEVIATION IN NUMBERS	D PE
		Green	White		
1	104	obs. 80 cal. 78	24 26	2	0.67
2	272	obs. 200 cal. 204	72 68	4	0.83
3	344	obs. 183 cal. 258	161 86	75.0	13.84
4	495	obs. 380 cal. 371.25	115 123.75	8.75	1.35
6	1106	obs. 843 cal. 829.5	263 276.5	13.5	1.38
7	87	obs. 60 cal. 65.25	27 21.75	5.25	1.93
10	502	obs. 266 cal. 376.5	236 125.5	110.5	16.90
9:7 ratio					
3	344	obs. 183 cal. 193.5	161 150.5	10.5	1.69
10	502	obs. 266 cal. 282.38	236 219.62	16.38	2.18

Families No. 5 and 8 were all pure green.

Five families out of nine segregated in a 3 to 1 ratio, two segregated in a 9 to 7 ratio and two were homozygous for green. This type of segregation would be obtained if one of the parents was heterozygous for two complementary factor pairs for green versus white seedlings and the other parent carried only one of these factor pairs in the heterozygous condition. In the F_1 a 3:1 ratio of green and white seedlings would be expected. In F_2 a ratio of 1 homozygous green to 3 segregating in a 3:1 ratio and two in a 9:7 ratio would be expected. The obtained ratios fit

the expected very well. The segregation of the immediate progeny of the parents of cross No. 58 are of interest although the numbers are small. Colsess II gave 21 green to 17 white seedlings and Colsess III 29 green to 10 white seedlings. Colsess II fits well to a 9 to 7 ratio while Colsess III fits a 3:1 ratio.

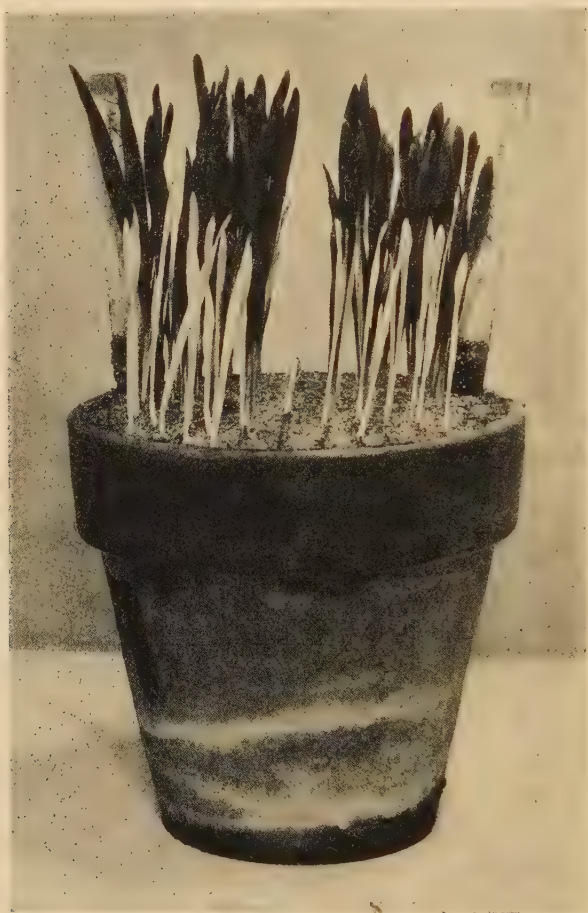


FIGURE 1.—White Seedlings in Colsess (right) and Trebi (left).

It is apparent that this strain of Colsess II carries two complementary factors for chlorophyll color. The strain will be studied more extensively for the purpose of isolating and obtaining linkage relations with the second white seedling factor.

White seedlings in Trebi

These were observed originally at the MINNESOTA STATION. A plant of this strain was grown in Colorado in 1924. Progenies of this plant were later grown in 1925, 1926, and 1927. As all the Trebi plants producing white seedlings are descendants of this single individual, the counts of seedlings made in the greenhouse and field from 1925 to 1927 are summarized together. In all, 829 seedlings have been counted, from parent plants heterozygous for green and white seedling factors; of these 616 were green and 213 were white. The expected ratio on a three to one basis for the above number of individuals is 621.75 green to 207.25 white. The obtained ratio deviates 5.75 from the expected. The deviation divided by the probable error (D/PE) is less than one which indicates that a single factor pair is involved. Phenotypically the white seedlings in Colsess and in Trebi I cannot be told apart (see figure 1).

Xantha seedlings in Colsess

This refers to yellow seedlings originally observed in a selection from Colsess, named Colsess IV. In the field the color is picric yellow (RIDGWAY, Plate IV). In the greenhouse the color is classified as Bright Chalcedony yellow by the use of RIDGWAY's tables (Plate XVII). This chlorophyll deficiency is modified in appearance by differences in temperature. As controlled conditions were not available, the definite thermal point for the development of chlorophyll was not learned. One plant of the xantha type was grown to maturity and the line continued for three generations. Seedling counts, of the progeny of parent plants which were heterozygous, were made both in the field and in the greenhouse. The following results were obtained:

TABLE 4
Segregation for green versus xantha in progeny of Colsess IV.

GREEN	XANTHA	DEVIATION IN NUMBERS	$\frac{D}{PE}$
1004	375	30.25	2.80

A single factor difference is responsible for the xantha seedling in Colsess IV.

Black versus white glume color

Studies were made in the following crosses: Colsess $\times$ *H. distichon nigrinudum*, Colsess $\times$ Minnesota 90-5, Colsess $\times$ Minnesota 90-8, and

Trebi $\times$ Minnesota 90-5. The results indicate that black *versus* white glume color are dependent upon a single factor pair. The following table gives the F_2 segregation of black and white glumed plants in the above crosses.

TABLE 5

Segregation for black versus white glumes in the F_2 of crosses between black and white glumed parents.

CROSS	F_2 DATA		DEVIATION IN NUMBERS	D — PE
	Black	White		
Colsess $\times$ H. dis. nig.	3531	1192	11.25	0.56
Colsess $\times$ Minn. 90-5	785	255	5.00	0.53
Colsess $\times$ Minn. 90-8	224	88	10.00	1.94
Trebi $\times$ Minn. 90-5	674	187	28.25	3.30

Hoods versus awns

Studies were made in crosses between Colsess $\times$ *H. distichon nigrinudum*, Colsess $\times$ *H. deficiens nudideficiens*, Colsess $\times$ Minnesota 90-5, and Colsess $\times$ Minnesota 90-8. The F_2 segregations approach a 3 to 1 ratio, indicating that a single factor pair is responsible for the hooded and awned condition. Table 6 gives the F_2 segregation of hooded and awned plants.

TABLE 6

Segregation of hooded versus awned plants in the F_2 of crosses between hooded and awned parents.

CROSS	F_2 DATA		DEVIATION IN NUMBERS	D — PE
	Hoods	AWNS		
Colsess $\times$ H. dis. nigrinudum	3471	1252	71.25	3.55
Colsess $\times$ H. def. nudideficiens	2650	987	77.75	4.38
Colsess $\times$ Minnesota 90-5	797	243	17.00	1.80
Colsess $\times$ Minnesota 90-8	229	83	5.00	0.97

Covered versus naked seeds

The covered versus naked seed character pair was studied in crosses between Colsess $\times$ *H. distichon nigrinudum* and Colsess $\times$ *H. deficiens nudideficiens*. Table 7 gives the F_2 segregation of plants from the above crosses for the covered seed versus naked seed character pair.

From the following table it appears that the covered versus naked condition of the seed is dependent upon a single factor pair difference.

TABLE 7

Segregation of covered versus naked seed in the F_2 generation of crosses between Colseß×*H. deficiens nudideficiens* and Colseß×*H. distichon nigrinudum*.

CROSS	F ₂ DATA		DEVIATION IN NUMBERS	D — PE
	Covered	Naked		
Colseß× <i>H. dis. nigrinudum</i>	3593	1130	50.75	2.53
Colseß× <i>H. def. nudideficiens</i>	2706	931	21.75	1.23

Long versus short haired rachilla

Studies were made in crosses between Colseß×*H. deficiens nudideficiens*, Colseß×Minnesota 90-5, Colseß×Minnesota 90-8, and Trebi×Minnesota 90-5. The segregation of the F_2 generation shows that long versus short haired rachillas differ by a single factor pair. The F_2 data are presented in table 8.

TABLE 8

Segregation of long versus short haired rachilla in the F_2 generation.

CROSS	F ₂ DATA		DEVIATION IN NUMBERS	D — PE
	Long	Short		
Colseß× <i>H. def. nud.</i>	2736	901	8.25	0.47
Colseß×Minn. 90-5	793	247	13.00	1.38
Colseß×Minn. 90-8	238	74	4.00	0.78
Trebi×Minn. 90-5	667	194	21.25	2.48

INHERITANCE OF FERTILITY OF THE LATERAL FLORETS

Studies were made in a cross between Colseß and *H. deficiens nudideficiens*. The F_1 generation was intermediate between six- and two-rowed. (Figure 2. No. 2.) The F_2 generation could not be classified accurately for fertility of the lateral florets. The progeny of the F_2 plants were grown in the F_3 , and the F_2 phenotypes were determined from the F_3 segregation. Seven groups were established which is a similar condition to that described by HARLAN and HAYES (1920). As six-row, two-row and *deficiens* have been found to be allelomorphic no attempt has been made in these studies to distinguish between two row and *deficiens*. The results establish the genotype of the six-rowed parent as consisting of two factor pairs for fertility of the lateral florets. Colseß is therefore represented as *vv II*. Factor *v* is similar to the *A* factor and *I* to the *B* factor of Harlan and Hayes. Similar segregations were found for the following crosses, Colseß×Minnesota 90-5 and Trebi×Minnesota 90-5. Table 9 presents

the observed and the calculated segregation on the genetic hypothesis outlined. While there is a slight deviation, there is in general good agreement between the observed results and the calculated.



FIGURE 2.—Types of F_1 heads obtained from crosses between Colseess $\times$ *H. distichon nigrinudum* (left) and Colseess $\times$ *H. deficiens nudideficiens* (right).

In a cross between Colseess and *H. distichon nigrinudum* the F_1 plants were intermediate, figure 2, No. 1. The F_2 plants were classified as six-rowed and non-six-rowed. The six-rowed class includes all F_2 plants

TABLE 9

Segregation in F₂, as determined by F₃ breeding behavior, for fertility of the lateral florets.

F ₂ GENOTYPE	CROSSES					
	Colsess×H. def. nud.		Colsess×Minnesota 90-5		Trebilcock×Minnesota 90-5	
	observed	calculated	observed	calculated	observed	calculated
<i>vvII</i>	83	88.7	148	123.3	110	119.2
<i>vvil</i>						
<i>vvi</i>						
<i>vVII</i>	99	88.7	121	123.3	113	119.2
<i>vVii</i>	50	44.4	48	61.6	65	59.6
<i>VVII</i>	19	22.2	27	30.8	34	29.8
<i>VVii</i>	39	44.4	48	61.6	61	59.6
<i>VvII</i>	45	44.4	73	61.6	58	59.6
<i>VVii</i>	20	22.2	28	30.8	36	29.8
Total	355	355	493	493	477	476.9
X ²		3.51		13.82		3.47
P		.7414		.0320		.7487

which produced only six rowed progeny in the F₃. Table 10 gives the F₂ segregation for non-six-rowed versus six-rowed.

TABLE 10

Segregation for non-six-rowed and six-rowed in the F₂ generation of a cross between Colsess and H. distichon nigrinudum.

SIX-ROWED	NON-SIX-ROWED	DEVIATION IN NUMBERS	$\frac{D}{PE}$
125	412	9.25	1.37

The segregation observed can be explained on the basis of single factor pairs for six-rowed versus non-six-rowed. No attempt was made to study the differences in the non-six-rowed group. Since the Colsess parent has been shown by previous crosses to contain the factor pair *vv* for six-rowed; the distichon parent has the gametic constitution *VV*.

INTERRELATIONS OF SIMPLE MENDELIAN CHARACTER PAIRS

Considerable information is already available regarding interrelations of genetic character pairs for the major botanical character differences. Consequently the interrelations for these will be presented briefly before giving the results of a study of the linkage relations of factor pairs for chlorophyll deficiencies with factor pairs for other character differences.

INTERRELATIONS OF CHLOROPHYLL DEFICIENCIES

White seedlings in Colsess and Trebi

Crosses were made between Trebi which was segregating for green and white seedling A_1a_1 and the heterozygous Colsess line called A_2a_2 . Only those crosses were considered where the parent plants by progeny tests were known to be heterozygous for factor pairs for green and white seedlings. Three separate crosses of this kind were available. The number of F_1 plants was 9, 2, and 11, respectively, and all were green, which indicates that the factor pair in Trebi for green and white seedlings is different from the A_2a_2 factor pair of Colsess. If the factor pairs are independently inherited, the calculated breeding behavior in F_2 is 1 pure green line, 2 heterozygous giving a ratio of 3 green:1 white and 1 segregating in a 9:7 ratio. The detailed results are given in table 11.

Of the 22 lines 6 were homozygous green, 9 agreed fairly well with a 3:1 ratio and 7 with a 9:7 ratio. In the 3:1 segregating lines there was a tendency for too few white seedlings. If there was linkage of the factor pairs for green versus white seedlings in Colsess and Trebi, it could be studied only in the lines where both factor pairs are involved. There is a consistent tendency for too few white seedlings in these lines, for linkage in the repulsion phase. The breeding behavior of the 22 F_2 lines is summarized in table 12. The agreement between observed and calculated for independent inheritance is good.

TABLE 12

The number of lines segregating in a 9:7 or a 3:1 ratio of green to white seedlings or producing only pure green seedlings.

	SEGREGATING LINES		PURE GREEN LINES
	9:7 ratio	3:1 ratio	
Number of lines	7	9	6
Calculated	5.5	11	5.5

It may be concluded, therefore, that the white seedlings in Trebi I are caused by the reaction of a different factor pair than A_2a_2 which is responsible for the white seedlings in Colsess. The factor pair for green and white seedlings of Trebi I will be represented as A_1a_1 .

White seedlings and xantha seedlings in Colsess

Crosses were made between lines which were heterozygous for the factor pairs A_2a_2 green versus white and X_2x_2 green versus xantha seedling.

Only those crosses were considered where both parent plants used proved to be heterozygous for the chlorophyll deficiencies which were being studied. In accordance with the factorial method used, $A_c a_c X_c X_c$ was crossed with $A_c A_c X_c x_c$. The F_1 seedlings were all green indicating that the factors causing white and xantha seedlings in Colsees are not allelomorphous. The F_1 plants should be of four different genotypes $A_c A_c X_c X_c$ producing only green seedlings in the F_2 ; $A_c A_c X_c x_c$ producing green and xantha seedlings in the proportion of 3:1; $A_c a_c X_c X_c$ producing seedlings in the ratio of 3 green to 1 white and $A_c a_c X_c x_c$ producing all three types of seedlings green, xantha, and white.

Forty-nine F_1 plants from crosses where both parents were heterozygous were obtained. The segregation for chlorophyll deficiencies was studied in F_2 . On the basis of the breeding behavior in F_2 , 13 F_1 plants proved homozygous for factors for green seedlings, 12 gave F_2 progeny segregating for green and xantha, 13 gave F_2 progeny segregating for green and white and 13 proved to be heterozygous for both the green versus xantha and green versus white factor pairs. This latter group gave an opportunity to study linkage relations of the two types of chlorophyll deficiencies. Because of the relatively few plants in the F_2 progenies it was necessary to make the study in F_3 . The study was made by growing the progenies of F_2 green plants from F_2 lines segregating for green, xantha and white seedlings.

The calculated segregation on the basis of independent inheritance of the factor pairs concerned is as follows: One plant out of every 9 should be homozygous for both dominant factor pairs and should breed true for green seedlings. Four plants would be heterozygous for 1 factor pair and homozygous for the other factor pair. Green and xantha seedlings would be produced by the progeny of two of these plants and green and white seedlings would be produced by the progeny of the other two. The four remaining plants would be heterozygous for both factors and would give progeny consisting of green, xantha, and white seedlings. There were 47 F_2 plants which matured in lines which in F_2 segregated for green, xantha and white seedlings. The genetic nature of these was determined by their F_3 breeding behavior. The calculated ratio for independent inheritance and for the four classes of plants described above is 5.22:10.44:10.44:20.88. If the factor pair $X_c x_c$ is inherited independently of the factor pair $A_c a_c$ only 21 of the 47 plants tested should give green, xantha and white seedlings.

The progeny of all 47 plants, however, gave green, xantha and white

seedlings. This indicates a possible linkage of factors for xantha (x_c) and white (a_c). An attempt was made to determine the crossover value from the F_3 seedling counts from the 47 F_2 plants.

All of the F_3 segregations were in the repulsion phase so the F_3 seedling counts of the 47 F_2 plants were summarized.

A short method has been derived to determine the expected number of lines which would give the coupling type of linkage in the F_3 generation if the repulsion type was obtained in the F_2 generation. By the use of Emerson's gametic ratio represented by $r:s$ these calculations can be made. In the case of repulsion s would be higher than r . By squaring r and s the expected number of F_3 lines showing repulsion and coupling would be obtained. The same method can be used to determine the number of lines which will show repulsion in the F_3 when coupling is obtained in the F_2 generation. An example is given below with 10 percent crossing over and repulsion: $r=1$, $s=9$; therefore 1 line would segregate in the coupling phase to 81 lines segregating in the repulsion phase.

Table 13 gives the summary of the segregations of the F_3 progeny of 47 green F_2 plants from the families heterozygous for both factors in the F_2 .

TABLE 13

The F_3 seedling counts of 47 green plants from the F_2 families heterozygous for both xantha and white seedlings from crosses between Colseess and Colseess IV.

CROSS	NO. OF F_2 GREEN PLANTS	F_3 SEEDLING RATIO				
		Green	Xantha	White	Total	X^2
Colseess $\times$ Colseess IV	35	8314	4120	3995	16531	
Colseess IV $\times$ Colseess	12	2869	1379	1460	5773	
Total	47	11183	5499	5455	—	
Observed ratio		11183	5499	5455	22304	
Calculated ratio		12546	4182	5576	22304	
						565.4

By examining the data in table 13, it will be seen that the xantha class has a larger number of individuals than the white class. This brings up the question: where do the double recessives belong? In a cross in which the same factor pair $X_c x_c$ was studied in relation to green versus white seedlings in Trebi $A_1 a_1$ the white class undoubtedly contained the double recessives. When a close examination of the individual lines in the Colseess crosses was made a variation was noticed in the number of xantha and white plants. Some lines were higher in white seedlings and others were

higher in xantha seedlings. When all lines are grouped a difference of 44 seedlings in favor of the xantha class out of a total of 10954 white and xantha seedlings was found. In the determination of the agreement between the calculated and observed ratios the double recessives have been considered as being included in the white class. It will be noted from table 13 that the fit of the observed ratio to the calculated 9:3:4 ratio is poor. $X^2=565.44$. Since the double recessive group cannot be separated from the white seedlings of the genetic constitution $a_c a_c X_c X_c$ and $a_c a_c X_c x_c$ it is not possible to use a formulae based on the double recessive group to determine the linkage value. Various crossover values were calculated and the different ratios compared with the observed. From the calculation it was found that the white class which contained the double recessive chlorophyll classes and simple recessive white group remained uniform for all degrees of linkage postulated. The X^2 method was used to determine the goodness of fit and good fits were obtained for crossover values between 12.5 and 4 percent.

TABLE 14

The observed and calculated ratio for various crossover percentages.

	CROSSOVER PER CENT	GREEN	XANTHA	ALBINO	X^2	P
Observed		11183	5499	5455		
Calculated	50	12546	4182	5576	565.44	.0000
"	20	11375.0	5352.96	5576	9.8520	.0074
"	12.5	11239.12	5488.87	5576	2.9232	.2343
"	12	11232.33	5495.63	5576	2.8458	.2455
"	11.1	11220.92	5507.20	5576	2.7550	.2587
"	10	11207.76	5520.24	5576	2.7621	.2576
"	9.1	11198.08	5529.29	5576	2.8189	.2494
"	8.3	11190.66	5537.24	5576	2.8938	.2386
"	4.76	11164.65	5563.36	5576	3.3738	.1903
"	4.	11160.92	5567.08	5576	3.4602	.1827

Further studies were made using the formulae presented by Collins (1) for use when there is difficulty in distinguishing any two classes. The

formulae used were $p = \sqrt{\frac{AB - 2Ab}{AB + Ab}}$ and $p = \sqrt{\frac{4AB - 2n}{n}}$. When p is

calculated from the ratio of AB to Ab¹ its value is 0.1053. When p is calculated from the ratio of AB to the total it equals 0.0745. When the above

¹ AB, Ab, aB, ab = the number of individuals in each of the four zygotic classes in a hybrid involving two character pairs Aa and Bb.

results are considered as crossover percentages values of 10.53 and 7.45 are obtained.

To further test the linkage relationship, the number of differently breeding F_3 lines which would be expected from the green plants of the F_2 families which segregated into green, xantha and white seedlings was calculated for independent inheritance and various degrees of linkage and compared with the observed ratio. The calculations were made from the following relationships based on Emerson's gametic ratio $r:s$

$$\begin{aligned} AA\ BB &= r^2 \\ AA\ Bb &= 2rs \\ Aa\ BB &= 2rs \\ Aa\ Bb &= 2s^2 + 2r^2 \end{aligned}$$

The calculated ratio of F_2 plants in each of the 4 genotypic groups $AA\ BB$, $AA\ Bb$, $Aa\ BB$, and $Aa\ Bb$ on the basis of independent inheritance is 1:2:2:4; for 10 percent crossing over 1:18:18:164 and for 4 percent crossing over 1:48:48:1154. Considering each of the middle classes as one, the ratios become: 0.5:1:1:2; 0.055:1:1:9.1; 0.0:1:1:24.04. When we compare the above ratios with the observed breeding behavior of F_3 families all 47 of which segregated for green, xantha, and white, it appears that the crossover value is less than 4 percent. In order to determine the value more accurately, larger numbers are needed. The above method seems to offer possibilities for testing the crossover percentage for crosses in which the double recessive cannot be separated and where the recessive and double recessive plants are lost before maturity. It appears very probable, however, that the factor pair $X_c x_c$ for green vs. xantha seedlings in Colsess is closely linked to the factor pair $A_c a_c$ for green versus white seedlings in Colsess. The crossover percentage is low.

White seedlings in Trebi with xantha seedlings in Colsess

Crosses were made between Trebi I which carries the factor pair $A_t a_t$ and Colsess IV which carries a factor pair for xantha seedlings $X_c x_c$. In the F_1 generation 31 seedling plants were pure green from crosses where both parents were known to be heterozygous for their respective chlorophyll deficient seedling factors indicating that white seedlings in Trebi and xantha seedlings in Colsess IV are caused by the interaction of genetic factors which are not allelomorphic. The progeny of twenty-nine F_1 plants were studied. Seven segregated for green, xantha, and white seedlings; 9 segregated for green and xantha seedlings; 5 segregated for green and white seedlings and 8 bred true for pure green seedlings. The F_1 plants

were very small and only a few seeds were obtained from each. In order to study the segregations with a larger number of seedlings, the progeny from the green plants from lines which segregated in F_2 for three types of seedlings were grown in F_3 . The breeding behavior of the progeny of 32 F_2 plants is given in table 15.

TABLE 15

F₃ breeding behavior of the progeny of the green plants from the F_2 families segregating in a 9:3:4 ratio.

13 Lines segregating in a 9:3:4 ratio						
OBSERVED RATIO			Calculated Ratio			X ²
Green	Xantha	White	Green	Xantha	White	
2872	848	1065	2691.6	897.2	1196.2	29.18
7 Lines segregating in a 3:1 ratio of green to xantha						
OBSERVED RATIO		Calculated Ratio		DEV. IN NUMBERS	D — PE	
Green	Xantha	Green	Xantha			
1730	560	1717.5	572.5	12.5	0.89	
6 Lines segregating in a 3:1 ratio of green to white						
OBSERVED RATIO		Calculated Ratio		DEV. IN NUMBERS	D — PE	
Green	White	Green	White			
1910	631	1905.75	635.25	4.25	0.29	
6 lines produced only pure green seedlings						

Any linkage, if present, would be studied in the 13 lines segregating for green, xantha, and white seedlings. If linkage were present it would be of the repulsion phase as in the previous cross. With linkage in the repulsion phase, the number of individuals in the middle or phenotypic classes Ab and aB would be high and the extreme classes or AB and ab would be low. In this cross the AB class is represented by the green seedlings and the Ab class by the xantha seedlings. The aB and ab classes or white seedlings are grouped and cannot be differentiated. Therefore with linkage in the repulsion phase the xantha seedlings should be higher than for independent inheritance and the green seedlings lower than calculated for independent inheritance. As this is not the case, however, as shown by the results given in table 15 it may safely be concluded that the

factor pairs A_1a_1 and X_cx_c are inherited independently. The agreement with a 9:3:4 ratio calculated for independent inheritance is not good. The number of chlorophyll deficient seedlings of both types are lower than the calculated. A certain amount of elimination of the seedlings which are recessive for chlorophyll deficiencies might explain this condition.

Further tests were made with the lines segregating in F_2 for green versus xantha and those segregating for green versus white seedlings. Progeny from heterozygous F_2 plants were grown in the F_3 and seedling counts made. The data are given in table 16.

TABLE 16

Summary of segregation for xantha and white seedlings in lines heterozygous for a single factor pair.

SEGREGATING FOR	OBSERVED		Calculated		DEVIATION IN NUMBERS	D — PE
	Green	Chlorophyll defective	Green	Chlorophyll defective		
C_cx_c	1353	366	1289.25	429.75	63.75	5.28
A_1a_1	3126	973	3074.25	1024.75	51.75	2.77

The number of xantha seedlings is lower than the calculated with a value of D/PE of 5.28.

INTERRELATIONS OF CHARACTER PAIRS FOR OTHER BOTANICAL CHARACTER DIFFERENCES

Black versus white glume color (Bb) and hoods versus awns (Kk)

Studies were made in crosses between Colseß $\times$ *H. distichon nigrinudum*, Colseß $\times$ Minnesota 90-5, and Colseß $\times$ Minnesota 90-8. The segregations obtained in the F_2 generation are given in table 17.

TABLE 17

Segregation in F_2 for black versus white glumes (Bb) and hoods versus awns (Kk) in crosses between Colseß $\times$ *H. distichon nigrinudum*, Colseß $\times$ Minnesota 90-5 and Colseß $\times$ Minnesota 90-8.

CROSS		BK	Bk	bK	bk	χ^2	P
Colseß $\times$ <i>H. dis. nig.</i>	obs.	2611	920	860	332	7.45	.0602
	cal.	2657	886	886	295		
Colseß $\times$ Minn. 90-5	obs.	603	182	194	61	1.67	.6479
	cal.	585	195	195	65		
Colseß $\times$ Minn. 90-8	obs.	166	58	63	25	2.41	.4983
	cal.	175.5	58.5	58.5	19.5		

In the cross between Colsess $\times$ *H. distichon nigrinudum* the number of awned plants in both the black and white glumed classes is higher than calculated on a 3:1 basis which explains the X^2 value of 7.45 with a P value of .0602. The chances that a deviation as high or higher may occur due to random sampling are 602 in 10000 trials or about 1 in 17. The other two crosses fit the expected ratio for independent inheritance very well. It can safely be concluded from the above data that black versus white glume color is caused by a factor pair inherited independently of the factor pair for hoods *versus* awns.

Black versus white glume color (Bb) and long versus short haired rachillas (Ss)

The results of three crosses, Colsess $\times$ Minnesota 90-5, Colsess $\times$ Minnesota 90-8, and Trebi $\times$ Minnesota 90-8 are given in table 18.

TABLE 18

Segregation in F_2 for black versus white glumes (Bb) and long versus short haired rachillas (Ss).

CROSS		BS	Bs	bS	bs	X^2	P
Colsess $\times$ Minn. 90-5	obs.	592	193	201	54	2.14	.5471
	cal.	585	195	195	65		
Colsess $\times$ Minn. 90-8	obs.	164	60	74	14	6.45	.0937
	cal.	175.5	58.5	58.5	19.5		
Trebi $\times$ Minn. 90-5	obs.	520	154	147	48	4.88	.1826
	cal.	484.3	161.4	161.4	53.8		

From the above data it is concluded that the factor pair for black and white glume is inherited independently of the factor pair which differentiates long *versus* short haired rachillas.

Black versus white glume color (Bb) and covered versus naked seed (Nn)

The factor pairs concerned were *Bb* and *Nn*. The results are given in table 19.

TABLE 19

*Segregation in F_2 for black versus white glumes (Bb) and covered versus naked seed (Nn) in a cross between Colsess and *H. distichon nigrinudum*.*

	BN	Bn	bN	bn	X^2	P
Observed	2679	852	914	279	3.26	.3578
Calculated	2657	886	886	295		

These data indicate that the factor pair for black *versus* white glume

color is inherited independently of the factor pair for covered *versus* naked seed.

Black versus white glume color (Bb) and non-six-rowed versus six-rowed (Vv)

Studies were made of the factor pairs *Bb* and *Vv* in a cross between Colseess and *H. distichon nigrinudum*. The F_2 plants were classified as six-rowed and non-six-rowed. Table 20 presents the data obtained in F_2 .

TABLE 20

Segregation in F_2 for non-six-rowed versus six-rowed (Vv) and black versus white glume color (Bb).

	<i>BV</i>	<i>bV</i>	<i>Bv</i>	<i>bv</i>	χ^2	<i>P</i>
Observed	304	108	88	37		
Calculated	302	100.7	100.7	33.6	2.48	.4856

BV = Black glume non-six-rowed

bV = White glume non-six-rowed

Bv = Black glume six-rowed

bv = White glume six-rowed

From the above data it may be concluded that the factor pair *Bb* for black *versus* white glume is inherited independently of the factor pair *Vv* for non-six-rowed *versus* six-rowed.

Hoods versus awns (Kk) and long versus short haired rachilla (Ss)

Studies were made in crosses between Colseess $\times$ *H. deficiens nudideficiens*, Colseess $\times$ Minnesota 90-5, and Colseess $\times$ Minnesota 90-8. Table 21 gives

TABLE 21

Segregation in F_2 for hoods versus awns and long versus short haired rachilla.

CROSS		<i>KS</i>	<i>Ks</i>	<i>kS</i>	<i>ks</i>	χ^2	<i>P</i>
Colseess $\times$ <i>H. def. nud.</i>	obs.	1983	667	753	234	9.87	.0198
	cal.	2046	682	682	227		
Colseess $\times$ Minn. 90-5	obs.	609	188	184	59	2.40	.4820
	cal.	585	195	195	65		
Colseess $\times$ Minn. 90-8	obs.	175	54	63	20	0.71	High
	cal.	175.5	58.5	58.5	19.5		

the observed and calculated ratios in the F_2 generation for hoods *versus* awns and long *versus* short haired rachilla. In the cross between Colseess and *H. deficiens nudideficiens* there is a wide deviation between the mono-

hybrid observed and calculated ratio for hoods *versus* awns. The awned group is higher than calculated and X^2 for a 9:3:3:1 ratio is 9.87. For this cross a calculated crossover value of 48.88 percent was obtained by Yule's coefficient of association Q (1924). A crossover value as high as this cannot be distinguished from independent inheritance with any degree of certainty in an F_2 generation. The value for P for the two other crosses indicates independent inheritance of the factor pairs for hoods *versus* awns and long *versus* short haired rachilla.

Hoods versus awns (Kk) and covered versus naked seed (Nn)

In crosses between Colsess $\times$ *H. distichon nigrinudum* and Colsess $\times$ *H. deficiens nudideficiens* a study was made of the interrelations of the factor pairs for hoods *versus* awns, Kk , and covered versus naked seed, Nn . Table 22 presents the F_2 data.

TABLE 22
Segregation in F_2 for hoods versus awns and covered versus naked seeds.

CROSS		KN	Kn	kN	kn	X^2	P
Colsess $\times$ <i>H. dis. nig.</i>	obs.	2635	836	958	294	8.88	.0313
	cal.	2657	886	886	295		
Colsess $\times$ <i>H. def. nud.</i>	obs.	1969	681	737	250	9.60	.0229
	cal.	2056	682	682	227		

In the above two crosses the awned plants are higher than calculated on a 3:1 basis which causes the dihybrid segregation to deviate widely from a calculated 9:3:3:1 ratio. The crossover value as obtained by the use of Q is 49.35 percent for the first cross and 49.20 percent for the second cross. The above crossover values cannot be considered as indications of linkage. However X^2 for the goodness of fit to a calculated 9:3:3:1 is 8.88 for the first cross and 9.50 for the second. P is .0313 and .0240 respectively. It can be concluded that the factor pair which causes the production of hoods *versus* awns is inherited independently of the factor pair which differentiates covered *versus* naked seeds.

Hoods versus awns (Kk) and non-six-rowed versus six-rowed (Vv)

In a cross between Colsess and *H. distichon nigrinudum* the interrelations were studied of the factor pairs, Kk for hoods *versus* awns and Vv non-six-rowed *versus* six-rowed. The F_2 plants were classified as six-rowed or non-six-rowed. In table 21 the different F_2 phenotypes are

represented by letters as follows: *KV* is hooded and non-six-rowed; *kV* is awned and non-six-rowed; *Kv* is hooded and six-rowed, and *kv* is

TABLE 23

Segregation in F₂ for hoods versus awns (Kk) and six rowed versus non-six-rowed (Vv).

	<i>KV</i>	<i>kV</i>	<i>Kv</i>	<i>kv</i>	χ^2	<i>P</i>
Observed	320	92	97	28	2.89	.4115
Calculated	302	100.7	100.7	33.6		

awned and six-rowed. The above data indicate that the factor pair for hoods *versus* awns is inherited independently of the factor pair for six-rowed *versus* non-six-rowed.

Long versus short haired rachilla (Ss) and covered versus naked seed (Nn)

Studies were made of the interrelations of the factor pairs *Ss* and *Nn* in a cross between Colless and *H. deficiens nudideficiens*. The F_2 data are presented in table 24.

TABLE 24

Segregation in F₂ for long versus short haired rachilla and covered versus naked seed.

	<i>SN</i>	<i>Sn</i>	<i>sN</i>	<i>sn</i>	χ^2	<i>P</i>
Observed	2061	675	645	256	5.79	.1242
Calculated	2046	682	682	227		

There is some deviation from the calculated 9:3:3:1 ratio. The genotypes of the parents of this cross were *NNss* and *nnSS*; therefore if linkage was present the *SN* and *sn* classes should have a similar number than is expected with independent inheritance which is not the case. The calculated value of *p* by Yule's Coefficient of Association was .4730. On these bases the conclusion may be made that the factor pair *Ss* for long and short haired rachilla and the factor pair *Nn* for covered and naked seed are inherited independently.

Covered versus naked seed (Nn) and non-six-rowed versus six-rowed (Vv)

The factor pairs *Nn* and *Vv* were studied in a cross between Colless and *H. deficiens nudideficiens*. Table 25 presents the F_2 data for covered *versus* naked seed and non-six-rowed *versus* six-rowed.

TABLE 25

Segregation in F₂ for covered versus naked seed and non-six-rowed versus six-rowed.

	VN	Vn	vN	vn	X ²	P
Observed	315	97	94	31	1.35	.7212
Calculated	302	100.7	100.7	33.6		

The data in table 25 indicate that the factor pair *Nn* is inherited independently of the factor pair *Vv*.

INTERRELATIONS OF CHLOROPHYLL DEFICIENCIES WITH
OTHER BOTANICAL CHARACTERS

*Green versus white seedlings (A₁a₁) and black versus
white glume color (Bb)*

In a cross between Trebi and Minnesota 90-5 the factor pairs studied were in the coupling phase. The Trebi parent was white glumed and carried the factor for white seedlings. The Minnesota 90-5 parent was black glumed and was homozygous for green seedlings. The F₂ segregation for green *versus* white seedlings and black *versus* white glumes is given in table 26.

TABLE 26

Segregation in F₂ for green versus white seedlings and black versus white glume color.

	A ₁ B	A ₁ b	a ₁ B—a ₁ b	X ²	P
Observed	447	68	157	40.01	very low
Calculated (9:3:4)	378	126	168		

The white seedling plants died and only the green plants survived to maturity. It will be observed that the white glumed class has fewer plants than are expected with independent inheritance and the fit to a calculated 9:3:4 ratio is very poor. Two of the classes were eliminated by the death of the white seedlings. To calculate the linkage value: Collins' formula

$$p = \sqrt{\frac{AB - 2Ab}{AB + Ab}}$$

in which the crossover value is calculated from two

classes was used. The crossover percentage obtained by this method was 22.29 percent. The observed data are compared with the theoretical on the basis of a crossover value of 22.29 percent (see table 27).

TABLE 27

Comparison of observed and calculated on the basis of a C. O. value of 22.29 per cent for the characters green versus white seedlings (A_1a_1) black versus white glumes in a cross between Trebi and Minnesota 90-5.

	A_1B	A_1b	$a_1B—a_1b$	CALCULATED CROSSOVER PERCENT	χ^2	P
Observed	447	68	157	22.29	1.00	.6065
Calculated	436	68	168			

The agreement between observed and calculated was good and apparently the factor pair A_1a_1 and Bb are linked.

Green versus white seedlings ($A_c a_c$) and black versus white glume color (Bb)

Crosses between Colseß $\times$ *H. distichon nigrinudum*, Colseß $\times$ Minnesota 90-5, and Colseß $\times$ Minnesota 90-8 were studied. Table 28 gives the observed and calculated ratio for the factor pairs concerned.

TABLE 28

Segregation in F_2 of green versus white seedlings $A_c a_c$ and black versus white glume color.

CROSS		$A_c B$	$A_c b$	$a_c B—a_c b$	χ^2	P
Colseß $\times$ <i>H. dis. nig.</i>	obs.	1953	690	812	5.88	.0537
	cal.	1943	648	864		
Colseß $\times$ Minn. 90-5	obs.	1283	408	518	3.53	.1766
	cal.	1243	414	552		
Colseß $\times$ Minn. 90-8	obs.	434	178	181	7.60	.0231
	cal.	446	149	198		

In this case as in other crosses the number of white seedlings is lower than calculated on a 3:1 basis. As no striking deviation is found in the other two classes it is evident that the factor pair for black versus white glume color is inherited independent of the $A_c a_c$ factor pair for chlorophyll development. It will be remembered that the factor pair in Colseß for green versus white seedlings, $A_c a_c$, was independent of that in Trebi, $A_1 a_1$, and that $A_1 a_1$ from Trebi was linked with a factor pair (Bb) for black versus white glumes.

Green versus white seedlings ($A_c a_c$) and hoods versus awns (Kk)

Studies were made in crosses between Colseß $\times$ *H. distichon nigrinudum*, Colseß $\times$ Minnesota 90-5 and Colseß $\times$ Minnesota 90-8. The cross was

made in the repulsion phase. If linkage is present the a_cK and A_ck classes would be larger than for independent inheritance. The plants having the recessive condition $a_c a_c$ would die in the seedling stage. With simple Mendelian independent inheritance and an absence of linkage a 9:3:4 ratio would be expected. Table 29 presents the expected and calculated ratios in F_2 .

TABLE 29

Segregation in F_2 for the characters green versus white seedlings and hoods versus awns.

		A_cK	A_ck	$a_cK—a_ck$	χ^2	P
Colsess $\times$ <i>H. dis. nig.</i>	obs.	1939	704	812	7.98	.0185
	cal.	1943	648	864		
Colsess $\times$ <i>H. def. nud.</i>	obs.	1053	397	479	4.43	.1135
	cal.	1085	362	482		
Colsess $\times$ Minn-esota 90-5	obs.	1269	422	518	2.84	.2463
	cal.	1243	414	552		
Colsess $\times$ Minn-esota 90-8	obs.	435	175	181	6.43	.0405
	cal.	446	149	198		

The above data gives a fair fit to the calculated ratio 9:3:4. There is a slightly higher number of individuals in the green awned class and a slightly lower number in the green hooded class than is expected with independent inheritance. This slight deviation is persistent in all four crosses and suggests a linkage with a high percentage of crossing over.

TABLE 30

F_2 segregations for green versus white seedlings and hoods versus awns and calculated linkage values for the different crosses.

CROSS	A_cK	A_ck	$a_cK—a_ck$	Calculated Crossover Percent
Colsess $\times$ <i>H. dis. nig.</i>	1939	704	812	44.82
Colsess $\times$ <i>H. def. nud.</i>	1053	397	479	42.26
Colsess $\times$ Minnesota 90-5	1269	422	518	50.13
Colsess $\times$ Minnesota 90-8	435	175	181	37.32
Total	4696	1698	1990	45.09

The calculated linkage value was obtained from Collins' formulae

$$p = \sqrt{\frac{AB - 2Ab}{AB + Ab}} \text{ for use when there is difficulty in distinguishing any two}$$

classes. Considerable variation was found in the calculated percentage of crossing over in the different crosses. The white seedling class is lower than calculated on a 3:1 basis and there is evidently some gametic elimination of the white seedling classes. The calculated results for independent inheritance was obtained from a gametic ratio for the factors for green and white seedlings of 1.0525 to 1. This ratio was calculated from the phenotypic ratio of green to white seedlings of 3.213:1 which was obtained from these crosses. In comparing observed with theoretical on the basis of 45.09 crossing over it was considered also that the functional gametes bearing the factors for green and white seedlings were in the ratio of 1.0525 to 1. The X^2 value for the linkage with 45.09 percent crossing over is .01 and P is very large while the X^2 value for independent inheritance is 8.17 with a P value of .0042 (see table 31).

TABLE 31

Observed and calculated ratios for independent inheritance and 45.09 percent crossing over.

RATIO	A_cK	A_ck	$a_cK \rightarrow a_ck$	X^2	P*
Observed	4696	1698	1990		
Independent inheritance	4795	1599	1990	8.17	.0042
45.09 percent crossing over	4692	1702	1990	.01	very large

* P was obtained from table of X^2 where $n=2$.

Green versus white seedlings ($A_c a_c$) and long versus short haired rachilla (Ss)

Studies were made in crosses between Colseß $\times$ *H. deficiens nudideficiens*, Colseß $\times$ Minnesota 90-5 and Colseß $\times$ Minnesota 90-8. Table 32 presents the F_2 segregation for green *versus* white seedlings and long *versus* short haired rachilla.

While some slight deviations from the calculated 9:3:4 ratio were found, no consistent variation was observed except for the classes of white seedlings which were lower than calculated in each case. The X^2 for the crosses between Colseß and the Minnesota selections was 4.02 and 5.61 with values of .1353 and .0624 respectively. In the cross between Colseß and *H. deficiens nudideficiens* the value of X^2 is 0.80, which gives a value of P which is very large. These data indicate that the factor pair $A_c a_c$ for green and white seedlings is inherited independently of the factor pair for long and short haired rachilla.

TABLE 32

Segregation in F₂ for green versus white seedlings and long versus short haired rachillas in crosses between Colsess×H. deficiens nudideficiens, Colsess×Minnesota 90-5 and Colsess×Minnesota 90-8.

CROSS		A_cS	$A_c s$	$a_c S—a_c s$	X^2	P
Colsess× <i>H. def. nud.</i>	obs.	1073	377	479	0.80	large
	cal.	1085	362	482		
Colsess×Minn. 90-5	obs.	249	442	518	4.02	.1353
	cal.	1243	414	552		
Colsess×Minn. 90-8	obs.	479	133	181	5.61	.0624
	cal.	446	149	198		

Green versus white seedlings (A_1a_1) and long versus short haired rachilla (Ss)

Studies were made in a cross between Trebi and Minnesota 90-5. The results are given in table 33.

TABLE 33

Segregation in F₂ for green versus white seedlings (A_1a_1) and long vs. short haired rachilla (Ss).

	A_1S	A_1s	$a_1S—a_1s$	X^2	P
Observed	388	127	157	0.98	large
Calculated	378	126	168		

The observed ratio fits the calculated 9:3:4 ratio very well, X^2 being 0.98. This indicates clearly that the factor pair A_1a_1 is inherited independently of the factor pair Ss .

Green versus white seedlings ($A_c a_c$) and covered versus naked seed (Nn)

The inheritance of the interrelations of green *versus* white seedlings and covered *versus* naked seeds were studied in crosses between Colsess × *H. distichon nigrinudum* and Colsess × *H. deficiens nudideficiens*. In the above crosses one parent was homozygous for the green seedling and naked seed factors and the other heterozygous for the factor pair for green *versus* white seedlings and homozygous for the covered seed factor. The F_2 segregation agrees well with the calculated ratio of 9:3:4, X^2 being 4.23 for the cross Colsess × *H. distichon nigrinudum* and 0.51 for the Colsess × *H. deficiens nudideficiens* cross. The calculated value of P was .1231 for the former and very large for the latter cross. (See table 34.)

TABLE 34
Segregation of F_2 for green versus white seedlings and cover versus naked seed.

CROSS		A_cN	A_cn	$a_cN—a_cn$	X^2	P
Colsess $\times$ <i>H. dis. nig.</i>	obs.	1975	668	812	4.23	.1231
	cal.	1943	648	864		
Colsess $\times$ <i>H. def. nud.</i>	obs.	1076	374	479	0.51	large
	cal.	1085	362	482		

It is evident from the above data that the factor pair $A_c a_c$ is inherited independently of the factor pair Nn .

*Green versus white seedling ($A_c a_c$) and non-six-rowed
versus six-rowed (Vv)*

This study of interrelations was made in a cross between Colsess $\times$ *H. distichon nigrinudum*. Table 35 gives the F_2 segregation for green [versus white seedlings and non-six-rowed versus six-rowed.

TABLE 35
Segregation of F_2 for green versus white seedlings and non-six-rowed versus six rowed.

	A_cV	A_cv	$a_cV—a_cv$	X^2	P
Observed	483	141	195	2.58	.2839
Calculated (9:3:4)	460.7	153.6	204.8		

The data presented in table 35 clearly indicate that the factor pair $A_c a_c$ is inherited independently of the factor pair Vv .

SUMMARY

1. Simple Mendelian inheritance was found for the following factor pairs: black versus white glume color (Bb), hoods versus awns (Kk), covered versus naked seed (Nn), non-six-rowed versus six-rowed (Vv), long versus short-haired rachilla (Ss), green versus white seedlings ($A_c a_c$), green versus white seedlings ($A_i a_i$) and green versus xantha seedlings ($X_c x_c$).

2. A two-factor difference was found for fertility of the lateral florets in crosses involving Colsess, a six-rowed barley, and *H. deficiens nudideficiens*, Colsess $\times$ Minnesota 90-5. Colsess evidently has the genetic constitution vv II while *H. deficiens nudideficiens* and Minnesota 90-5 the genetic constitution VV ii.

3. Three genetically different seedling chlorophyll deficiencies are inherited as simple Mendelian recessives. These chlorophyll deficiencies are designated as follows: white $a_i a_i$, white $a_c a_c$, and xantha $x_c x_c$.

4. Two complementary factors for chlorophyll production were found in a strain of Colsees. One factor pair was found to be $A_c a_c$; further studies will be made with the other pair.

5. Independent Mendelian inheritance was found between the following character pairs: black versus white glume color, hoods versus awns, covered versus naked seed, non six-rowed versus six-rowed, and long versus short-haired rachilla.

6. Studies of the interrelation of chlorophyll deficiencies and other characters indicate two probable linkage groups:

- (a) Green *versus* white seedlings $A_c a_c$, green *versus* xantha seedlings $X_c x_c$, and possibly hoods *versus* awns Kk .
- (b) Black *versus* white glume color Bb and green *versus* white seedlings $A_i a_i$.

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